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Linking indices for biodiversity monitoring to extinction risk theory

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1   **Linking indices for biodiversity monitoring to extinction risk**

2   **theory**

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11

12   **Abstract**

13   Biodiversity indices often combine data from different species when used in

14   monitoring programs. Heuristic properties can suggest preferred indices, but we lack

15   objective ways to discriminate between indices with similar heuristics. Biodiversity

16   indices can be evaluated by determining how well they reflect management objectives

17   that a monitoring program aims to support. For example, the Convention on

18   Biological Diversity requires reporting about extinction rates, so simple indices that

19   reflect extinction risk would be valuable. Here we develop three biodiversity indices

20   that are based on simple models of population viability that relate extinction risk to

21   abundance. The first index is based on the geometric mean abundance of species. A

22   second uses a more general power mean. A third integrates both the geometric mean

23   abundance and trend. These indices require the same data as previous indices, but

24   they also relate directly to extinction risk. Field data for butterflies and woodland

25   plants, and experimental studies of protozoan communities show that the indices

26   correlate with local extinction rates. Applying the index based on the geometric mean

27   to global data on changes in avian abundance suggests that the average extinction

28   probability of birds has increased approximately 1% from 1970 to 2009.

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31

32   **INTRODUCTION**

33   The importance of biodiversity for a healthy and equitable society has been

34   acknowledged by over 190 countries that ratified the Convention on Biological

35   Diversity (CBD). The convention has a specific target to reduce the extinction risk of

36   species (Secretariat of the Convention on Biological Diversity 2010), so monitoring of

37   species extinction is important. Reporting actual extinctions, while potentially

38   informative, is retrospective, whereas the convention and many other biodiversity

39   programs seek to reduce future extinctions. Further, retrospective assessments are

40   subject to error because the fate of species is known imprecisely (Collar 1998; Keith

41   & Burgman 2004; Rout et al. 2010). Hence, biodiversity monitoring programs would

42   be more valuable if they can be interpreted in terms of extinction risk.

43   Changes in the assessed risk to species can contribute to biodiversity monitoring. For

44   example, the IUCN Red List is used to calculate the Red List Index (RLI, Butchart et

45   al. 2007), one of four global indicators of biodiversity status and trends approved by

46   the CBD (Jones et al. 2011). The relationships of the other three indicators (extent of

47   forest; protected-area coverage; and the Living Planet Index, LPI, Jones et al. 2011) to

48   extinction risk are not explicit.

49   Buckland et al. (2005) identified three aspects of species diversity that are of primary

50   interest when monitoring changes over time: number of species, overall abundance

51   and species evenness, from which they derived six desirable criteria for an index of

52   biodiversity based on abundance data. On evaluating several proposed indices against

53   these criteria, the geometric mean of relative abundances was one of only two that

54   met all six criteria, with van Strien et al. (2012) lending further support to the

55   geometric mean.

56   While we agree with the heuristic properties used to assess different indices of

57   biodiversity, a good index should also be clearly related to particular management

58   objectives or biodiversity outcomes. For example, where extinction risk is the

59   management concern, understanding how the index reflects changes in this risk would

60   be desirable. In the absence of a single measurable definition of biodiversity

61   (Secretariat of the Convention on Biological Diversity 2010; Jones et al. 2011), we

62   aim to examine how abundance data might be used to monitor extinction rates of

63   species for the purposes of reporting under the CBD and other biodiversity programs.

64   Here, we use simple models of population viability to develop three indices of

65   extinction risk based on abundance data. These indices are designed to have the same

66   data requirements as those considered by Buckland et al. (2005), but with the

67   additional benefit of being directly related to extinction risk. We evaluate the indices

68   using simulation, field data on local extinctions of butterflies and woodland plants,

69   and experimental data on protozoan communities. Finally, we interpret changes in the

70   LPI in terms of changes in the average probability of extinction of species.

71   **Methods**

72   The indices are derived from simple models of population viability, using clearly

73   articulated assumptions that can be tested. First, consider the case when the long-term

74   average population growth of each species is negative. If we assume that each species

75   is experiencing deterministic exponential decline, then

76    $x(t) = x(0)\lambda^t$,

77   where $x(t)$ is population abundance at time t, and λ is the growth parameter ($\lambda < 1$ for

78   a declining population). It is then straightforward to calculate that extinction (such

79   that $x(t) = 1$) occurs at time $T = -\ln[x(0)]/\ln[\lambda]$. If the long-run growth rate is

80   negative, then for stochastic population models the mean extinction time is also

81   approximately logarithmically dependent on initial population size (Lande 1993).

82   With the simplifying assumption that the rate of decline is the same for each species

83   (we address this particular assumption later), the mean expected time to extinction,

84   averaging over n species, is proportional to the mean of the logarithm of population

85   abundance. As we show below, the mean expected time to extinction is proportional

86   to the logarithm of the geometric mean of population abundances (M_0);

87    $$\overline{T} \propto \overline{\ln(x)} = \frac{1}{n}\sum_{i=1}^{n}\ln(x_i)$$

88    $$= \ln\left(\left[\prod_{i=1}^{n}x_i\right]^{1/n}\right)$$

89    $$= \ln(M_0).\tag{1}$$

90   Equation 1 relates the mean time to extinction to the geometric mean abundance.

91   However, it would be helpful to determine how this index might relate to the

92   proportion of species going extinct. We approximate this by assuming that times to

93   extinction have an exponential distribution. The proportion of species going extinct

94   within time t is then $1 - \exp(-t/\overline{T})$. When this proportion is ≤ 0.2, it can be

95   approximated by $t/\overline{T}$, leading to:

96    $$I_g = \frac{1}{\ln(M_0)}.\tag{2}$$

97   This index should correlate linearly with the proportion of species going extinct under

98   the assumptions stated above. The approximation of $1 - \exp(-t/\overline{T})$ by $t/\overline{T}$ will tend to

99   lead to non-linearity (but a monotonic relationship) for higher risks.

100   We develop a second index based on a different set of assumptions. We consider a

101   stochastic population model in which the logarithm of the population growth rate has

102   a normal distribution with a mean of zero and variance σ^2. For this model, the risk of

103   extinction within a given time period t is (Ginzburg et al. 1982; Dennis et al. 1991;

104   McCarthy & Thompson 2001):

105   $q_i(x_0) = 2\varphi(-v)$.

106   where $\varphi()$ is the standard normal cumulative distribution function, $v = -\ln(1/x_0)/(\sigma\sqrt{t})$

107   and x_0 is the initial population size. This functional form could be used as an index,

108   but it does not provide a simple numerical solution. Instead, we approximated this

109   equation by a function of the form $A\,x^{-B/(\sigma\sqrt{t})}$ (by approximating $\log(q_i(x_0))$ as a linear

110   function of $\log(x)$) with the values of A and B depending on the value of the extinction

111   risk. For small extinction risks, $q_i <\approx 0.15$, $A = 2.2$ and $B = 1.87$ provide a good

112   approximation. When the extinction risk is close to one, a better approximation is A

113   $=1$ and $B = 0.798$. Regardless, the probability of extinction scales approximately with

114   abundance in proportion to x^{-b}, with $b = B/(\sigma\sqrt{t})$. Thus, averaged across n species, we

115   would expect the proportion of species going extinct to be

116   $$L = \sum_{i=1}^{n} q_i / n = k \sum_{i=1}^{n} x_i^{-b} / n = k(M_{-b})^{-b},\qquad\qquad (3)$$

117   where k is a constant of proportionality and M_{-b} is a power mean of abundance with

118   power $p = -b$,

119 $$M_{-b} = (\frac{1}{n}\sum_{i=1}^{n}x_i^{-b})^{-1/b}.$$

120 Consequently, our second index is based on a power mean of abundance:

121 $$I_b = (M_{-b})^{-b}. \qquad (4)$$

122 The value of b depends on the time horizon over which risks are assessed. If we

123 consider a time horizon of $T=100$ years and a standard deviation of $\sigma = 0.1$ (Dennis et

124 al. 1991), the extinction risk of each species is likely to be relatively small (recall,

125 zero mean growth rate), and b would be of the order $1.8 \approx 2$. The value of b will be

126 larger for shorter time horizons.

127 A third index can be derived from the deterministic model that accounts for the

128 population growth rate, in addition to population size. Noting again that the mean

129 time to extinction under deterministic decline is $-\ln[x(0)]/\ln[\lambda]$, then the proportion of

130 species going extinct can be approximated by $-\ln[\lambda]/\ln(M_0)$, allowing communities

131 with different population growth rates of species to be compared. Using the mean of

132 the logarithmic population growth rate of species within a community, μ_r, as the

133 estimate of $\ln[\lambda]$ leads to the index:

134 $$I_t = \frac{-\mu_r}{\ln(M_0)}. \qquad (5)$$

135 This index requires extra data, being the population growth rates of species within the

136 community. Such data might be uncommonly available, but are necessary to compare

137 risks among communities where the species are declining at different rates.

138 **Simulations for evaluating indices**

139   We simulated stochastic species dynamics within communities to evaluate the

140   correlation between the different indices and the proportion of species going extinct.

141   Each community consisted of 500 species, and there were 100 different communities.

142   For each species j in community i, we simulated the population dynamics over 20

143   time steps using the exponential growth model such that the population size in time

144    $t+1$ is given by:

145    $x_{ijt+1} = \lambda_{ijt}x_{ijt}.$

146   Parameter values for the 100 different communities were chosen such that the

147   proportion of species going extinct spanned a wide range (in our case between 0.02

148   and 0.64). Within each community, the initial population size $\ln x_{ij0}$ was drawn from a

149   lognormal distribution with mean μ_N and coefficient of variation c_N, and the

150   logarithmic growth rate $\ln \lambda_{ijt}$ was drawn from a normal distribution with mean μ_r and

151   standard deviation σ_r. The proportion of 500 species that fell to or below one

152   individual measured the average extinction risk of the community.

153   To ensure that each community had different initial population sizes and different

154   trends in abundance (and hence different average extinction risks), the mean and

155   coefficient of variation of the population size (μ_N and c_N) and the mean and standard

156   deviation of population growth rate (μ_r and σ_r) of each was varied among

157   communities. The coefficient of variation c_N was drawn from a uniform distribution

158   on the interval [0.5, 3.0]. The mean population size was equal to $1.2^d 100$, where d was

159   drawn from a uniform distribution on the interval [0, 20], so mean population size

160   varied among communities over the interval [100, 3834]. The mean population

161   growth rate (μ_r) was drawn from a uniform distribution on the interval [−0.3, −0.1],

162   and the standard deviation (σ_r) was drawn from a uniform distribution on the interval

163   [0.05, 0.4]. To test how differences in abundance, rather than population trend,

164   influence the performance of the indices, data were also simulated with μ_r set to –0.2

165   for all communities.

166   The three indices of extinction risk (I_g, I_b and I_t) were calculated for the simulated

167   communities and the correlations between these and the proportion of species going

168   extinct was examined. The performance of the arithmetic mean abundance and the

169   modified Shannon diversity index of Buckland et al. (2005), other putative

170   biodiversity measures, were also examined for the simulated data. For these two

171   cases, we multiplied the indices by −1 so that the indices would be expected to be

172   positively correlated with extinction risk.

173   **Data for evaluating indices**

174   The correlation between the indices and local extinction risk was evaluated using field

175   data on Lepidopetera (Krauss et al. 2003) and woodland plants (Sutton & Morgan

176   2009). Because data on population trends were unavailable for these datasets, only

177   eqns 2 and 4 were evaluated. We evaluated all three indices with data from

178   experimental protozoan communities (Clements et al. 2013). The original publications

179   detail the data and its collection; some information is provided here for context (see

180   also Supporting Information). The data sets we examined reported both extinctions of

181   multiple species and information on initial abundances.

182   Each dataset included information on the abundance of each of the species in replicate

183   local communities at a particular point in time, and data on the proportion of those

184   species that went extinction over a subsequent period of time. For the protozoan

185   community, estimates of abundance were available at multiple points in time prior to

186   the period over which extinctions were assessed. For each dataset, we calculated the

187   indices using the abundance data (and the trend data in the case of the index I_t for the

188   protozoan dataset).

189   For each dataset, we calculated the correlation (with 95% confidence interval based

190   on a z-transformation; Sokal & Rohlf 1981) between the value of each index and the

191   proportion of species in each community going extinct. We also determined, via

192   simulation, the correlations that would be expected if each index were perfectly

193   correlated with extinction of species, while accounting for the finite number of

194   species in each community (Supporting Information). This allowed us to determine

195   whether the observer correlations were substantially different from what would be

196   expected given the limitations of the datasets.

197   **Relating I_g to the Living Planet Index**

198   The LPI is the geometric mean abundance of vertebrate species in a particular year

199   divided by the geometric mean in 1970 (Loh et al. 2005; Collen et al. 2009).

200   Therefore, the index based on the geometric mean can be related to the LPI simply as

201    $I_g = 1/\ln(c \, \text{LPI})$, where c is the geometric mean abundance in 1970. If I_g is

202   proportional to the probability of extinction, as assumed in its derivation, LPI values

203   can be converted to proportional changes in the probability of extinction of species,

204   which will equal $-\ln(\text{LPI}) / [\ln(c) + \ln(\text{LPI})]$. We calculated this quantity for the

205   world's birds based on published avian LPI values (Baille et al. 2010).

206   These proportional changes depend on c, which is not well known. The arithmetic

207   mean abundance of birds is thought to be approximately 10 million individuals per

208   species but, because species abundance distributions are heavily right-skewed, the

209   geometric mean will be substantially less (Gaston & Blackburn 2003). We estimated

210   the global species abundance distribution of birds, and hence the geometric mean, by

211   fitting a log-normal distribution to data on reported population size for the global list

212   of 1253 threatened species on BirdLife International's website

213   (http://www.birdlife.org/datazone/species/search; accessed 20 December 2011) and

214   assuming an arithmetic mean of 10 million birds per species. We assumed that

215   abundances of the remaining 8663 non-threatened species were greater than 1000. In

216   this case, and in cases where the data on threatened species were provided as ranges,

217   we fitted the model assuming censored data. When an upper limit was not provided,

218   we set the upper limit of 10 billion individuals for each species, which is greater than

219   the reported abundance of passenger pigeons, the world's most abundant bird prior to

220   its extinction. The geometric mean of the resulting log-normal probability distribution

221   was then calculated. The sensitivity of the results to the calculated value of c was

222   examine by varying c by one order of magnitude and re-calculating the proportional

223   changes in the probability of extinction.

224   **Results**

225   For the simulated communities with variation in mean growth rate among

226   communities, the index based on the power mean (I_b) and the index based on the

227   geometric mean (I_g) were positively correlated with the proportion of species going

228   extinct (Pearson product moment correlations $r = 0.39$ and $r = 0.50$, respectively).

229   Spearman rank correlations were similar ($r_S = 0.34$ and 0.49 respectively). Variation

230   in mean growth rates among communities explained much of the imperfect

231   correlations; correlations for the index that is based on population trend were high ($r =$

232   0.96; $r_S = 0.99$ for I_t), and were similarly high for the geometric mean index (I_g) when

233   all communities had the same mean rate of decline ($r = 0.97$ when $\mu_r = -0.2$ for all

234   communities).

235   The index based on the geometric mean (I_g) and the index that considers population

236   trend (I_t) were more strongly correlated with the proportion of species going extinct

237   than either index based on the arithmetic mean or the Shannon diversity ($r = 0.44$ in

238   both cases when $\mu_{r,i}$ varied on the interval [$-0.3, -0.1$], and $r = 0.94$ and 0.91

239   respectively when $\mu_{r,i}$ was -0.2 for all communities). The index based on the power

240   mean (I_b) was the least strongly correlated with the proportion of species going extinct

241   ($r = 0.39$ when the mean population growth rate varied among communities, $r = 0.66$

242   when it was consistent); this might be expected given the strong influence of the

243   population trend on the simulated extinction risks, whereas the index I_b assumed no

244   trend. Note, the derivation of I_g included a trend, but it dropped out of the calculation

245   of the index as a proportionality constant by assuming the same trend for all

246   communities.

247   For the real communities, the index based on the geometric mean abundance (I_g) and

248   the index based on the power mean (I_b) were positively correlated with the proportion

249   of Lepidopetera and woodland plant species that went extinct (Fig. 1a,c; Fig. 2). The

250   95% confidence intervals for these correlation coefficients did not encompass zero. In

251   contrast, the correlations for these indices were negative for the protozoan dataset

252   (Fig. 1e,f), although the correlation for the index that included population trends was

253   positive ($r=0.33$; Fig. 1g, Fig. 2). In this dataset, abundances were similar for most

254   communities, so the indices spanned a narrow range of values. The 95% confidence

255   intervals for the correlation coefficient were wide (Fig. 2), so the strength of the

256   relationship could not be determined reliably for the protozoan dataset.

257 There was only one case (the index based on the power mean for the protozoan

258 dataset) that the observed correlation coefficient was both not significantly different

259 from zero (Fig. 2) and substantially less than the correlation coefficient that might be

260 expected even if the indices were perfectly correlated with the proportion of species

261 going extinct (Fig. S1). In the other cases, either the 95% confidence intervals of the

262 observed correlations were greater than zero (Fig. 2), or the observed correlations

263 were consistent with the range of values that might be expected (Fig S1).

264 The geometric mean abundance (c) of birds was estimated to be approximately

265 100,000 individuals per species. Assuming that the index based on the geometric

266 mean is proportional to the extinction risk of species at the global scale, the reported

267 decline in the LPI for birds from 1970 to 2009 of 13% (Baille et al. 2010) reflects a

268 proportional increase in the probability of extinction of approximately 1% for values

269 of c between 10,000 and 1,000,000 (Fig. 3). Smaller values of c imply larger changes

270 in the risk of extinction for a given change in LPI, although the results are relatively

271 insensitive to the choice of c (Fig. 3), and are primarily driven by the LPI values (Fig.

272 S2).

273 **Discussion**

274 We derived indices that can be interpreted in terms of changes in extinction risk. By

275 deriving the indices from theoretical population models, the merits of possible

276 alternative indices can be assessed to determine which indices are best supported by

277 data. Our analysis shows that the indices are positively correlated with the proportion

278 of species going extinct in small patches, despite highly simplified assumptions used

279 to build the indices.

280   In addition to the heuristic properties that Buckland et al. (2005) and van Strien et al.

281   (2012) used to assess different indices of biodiversity, a good index should also be

282   clearly related to particular management objectives. For example, we have shown that

283   the geometric mean abundance of species, which has good heuristic properties

284   (Buckland et al. 2005; van Strien et al. 2012), can be related to the proportion of

285   species within an area that are likely to become extinct. This lends much greater

286   support to this index as a biodiversity metric.

287   The geometric mean abundance of species is used increasingly, including in North

288   American and European bird monitoring (Gregory & van Strien 2010; Butchart et al.

289   2010) and for planning fire management (Di Stefano et al. 2013). The LPI for

290   reporting the state of species is the geometric mean abundance in each period, divided

291   by the geometric mean abundance in the first time period (Loh et al. 2005; Collen et

292   al. 2009). The LPI is based on the notion that changes in species abundance are

293   important, but was not derived directly from ecological theory. We do not intend this

294   as a particular criticism of the LPI, which has more support than some alternative

295   indices, but we argue that ecological indices should have sound theoretical

296   foundations. A theoretical foundation helps make the meaning and scope of the index

297   clearer and more easily justified. For example, the derivation of the index based on

298   the geometric mean implies that reductions in the LPI can be interpreted in terms of

299   an increased average probability of extinction of the species. We estimate that the

300   reduction of the global avian LPI of approximately 13% between 1970 and 2009

301   corresponds to approximately a 1% increase in the probability of extinction (Fig. 6).

302   This is less than the increased risk of 7% implied by the Red List Index (RLI) of birds

303   for the period 1988 to 2004 (Butchart et al. 2004), which is the only CBD index that is

304   related directly to extinction. The larger increase in extinction risk implied by the RLI

305   compared with I_g might be expected given the RLI's focus on threatened species.

306   The indices based on the power mean (I_b) and geometric mean (I_g) have the same data

307   requirements as those considered by Buckland et al. (2005). That is, they require

308   information on the abundance of a suite of species at a particular point in time. The

309   index that accounts for different trends among communities, (I_t) requires additional

310   information (the average trend of the species in the community). Such data will tend

311   to be available for only a subset of species, and this subset is likely to be a biased

312   sample of relevant species in a community. Any bias will be common to all indices,

313   with the consequence that they might not broadly represent all possible species of

314   interest.

315   Using a theoretical foundation to develop indices suggests ways in which the indices

316   can be evaluated and improved, and assumptions underlying the indices are clear. The

317   clear assumptions can be tested individually to determine whether they are violated in

318   particular circumstances and the consequences of those errors. Further, the overall

319   properties of an index can be assessed against data if it approximates an explicit

320   quantity. In our case, we sought an index that would be linearly correlated with the

321   proportion of species becoming extinct such that a change in the index would reflect a

322   particular change in the proportion of species going extinct. The clear assumptions

323   help highlight how the indices could be modified.

324   As an example of modification, trends in population size are likely to influence

325   extinction risks. The index that incorporates trend (I_t) shows how abundance and trend

326   might be incorporated into a single index if the assumption of a consistent trend

327   among communities is not supported. In the case of the experimental protozoan

328 community, an assumption of an equal trend is clearly not supported. Of the four

329 protozoan species, one went extinct in all 40 experimental replicates, and one

330 persisted in all replicates. Thus, the proportion of species in each community that

331 went extinct was influenced substantially by the identity of the species, which had

332 different trends not just different population sizes.

333 Biodiversity indices, such as those developed here, will be sensitive to the choice of

334 species that are included. For example, species included in the LPI calculations are

335 not a random sample of all possible species, with biases likely. Unless the scheme

336 used to select the sample of species used in the index is considered carefully, it will be

337 unclear how the selected species will represent the broader suite of biodiversity.

338 Factors other than those included in the indices are likely to influence extinction. The

339 Lepidoptera species will be differentially susceptible to apparent local extinction

340 because of different dispersal and abilities to persist outside the focal habitat patches.

341 Other species will occur only ephemerally in the patches, reducing the influence of

342 abundance on local extinction. However, the results were qualitatively identical when

343 analysing only strict grassland specialists, so we reported only the results for the

344 larger collection of species.

345 Our indices were based on models of exponential decline of single populations,

346 thereby ignoring spatial aspects and density-dependence. Other indices based on

347 metapopulation dynamics, for example, could be developed to account for spatial

348 effects. Indeed, metapopulation capacity, which is derived from colonisation and

349 extinction dynamics of habitat patches (Day & Possingham 1995; Hanski &

350 Ovaskainen 2000), can be viewed as an index of metapopulation persistence

351 (Moilanen & Nieminen 2002). Density-dependence might be less important for

352   populations that are declining deterministically, although accounting for non-

353   exponential decline might be important because temporal patterns of decline influence

354   risk (Di Fonzo et al. 2013).

355   Imprecise estimation of abundance (particularly in the woodland case study), some

356   residual uncertainty about the local extinction of species due to imperfect detection,

357   and the false assumption of equivalent dynamics of all species would all weaken the

358   correlation between the indices and the observed extinction rate. Despite this, the

359   predicted and observed extinction risks were correlated (Figs 1-3). This implies that

360   using the indices to aggregate data across species is reasonable. However, further tests

361   of the indices to predict local extinction would be valuable, as would evaluating

362   extinction risk over regions larger than just single patches (e.g., based on spatial

363   population dynamics).

364   The index based on the power mean is sensitive to the choice of the parameter b, and

365   estimating it via estimates of the standard deviation of the population growth rate (σ)

366   might be difficult. Thus, the indices based on the geometric mean (I_g and I_t) might be

367   more appealing because a freely-varying parameter does not require estimation.

368   Further, extinctions might be dominated by deterministic declines rather than random

369   fluctuation around a zero mean growth rate. If true, the indices based on the geometric

370   mean might be preferred over that based on the power mean.

371   The SAFE index (Clement et al 2011; see also Akçakaya et al. 2011; Beissinger et al.

372   2011; McCarthy et al. 2011) is essentially equal to the logarithm of population size.

373   Our analysis shows, therefore, that the SAFE index will be proportional to the

374   expected time to quasi-extinction (time to reaching a given threshold). But it also

375   shows that the SAFE index will be comparable among species as a measure of threat

376   only if trends in population size of those species are similar. Where trends differ

377   among species, an index based on $-\ln[x(0)]/\ln[\lambda]$ is likely to better reflect threat.

378   Further, prioritization of management, which apparently motivated the SAFE index,

379   should not be based on extinction risk, but on the ability to change risks (McCarthy et

380   al. 2011). This might be assessed, for example, by the relative cost of changing $x(0)$ or

381   λ and their influence on $-\ln[\lambda]/\ln[x(0)]$ (Baxter et al. 2006).

382   An index developed without theory does not mean it will have poor properties. As we

383   have seen, the geometric mean was developed without theory but appears to have

384   useful properties (Buckland et al. 2005; van Strien et al. 2012). The demonstrated

385   relationship to extinction risk lends further support to the geometric mean. Our

386   analysis also indicates how the geometric mean might incorporate population trends.

387   We suggest that biodiversity indices should be developed more frequently from

388   theoretical foundations to provide more explicit links between the index, the data

389   underlying the index, and the meaning of changes in the index. Such indices will

390   inevitably exclude factors that might be important; this is a feature of any model.

391   However, stronger theoretical foundations for biodiversity indices would clarify the

392   features that are considered and those that are ignored, and would allow the indices to

393   be more easily evaluated and improved.

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400 comments on a draft manuscript.

401 **Supporting Information**

402 Further details on the datasets used (Appendix S1), details on calculating the expected

403 correlation (Appendix S2), and Figs S1 and S2 are available online. The authors are

404 solely responsible for the content and functionality of these materials. Queries (other

405 than absence of the material) should be directed to the corresponding author.

406 **Literature Cited**

407 Akçakaya, H.R., G. M. Mace, K. J. Gaston, H. Regan, A. Punt, S. H. M. Butchart, D.

408 A. Keith, and U. Gärdenfors. 2011. The SAFE index is not safe. Frontiers in

409 Ecology and Environment **9**:485-486.

410 Baillie, J. E. M., J. Griffiths, S. T. Turvey, J. Loh, and B. Collen. 2010. Evolution

411 Lost: Status and Trends of the World's Vertebrates. Zoological Society of

412 London, UK.

413 Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. W. Menkhorst, and N.

414 McLean. 2006. Accounting for management costs in sensitivity analyses of matrix

415 population models. Conservation Biology **20**:893-905.

416 Beissinger, S. R., C. H. Flather, G. D. Hayward, and P. A. Stephens. 2011. No safety

417 in numbers. Frontiers in Ecology and Environment **9**:486.

418 Buckland, S. T., A. E. Magurran, R. E. Green, and R. M. Fewster. 2005. Monitoring

419 change in biodiversity through composite indices. Philosophical Transactions of

420 the Royal Society B-Biological Sciences **360**:243-254.

421   Butchart, S. H., H. R. Akçakaya, J. Chanson, J. E. Baillie, B. Collen, S. Quader, W. R.

422   Turner, R. Amin, S. N. Stuart, C. Hilton-Taylor. 2007. Improvements to the Red

423   List Index. PLoS ONE **2**(1): e140. doi:10.1371/journal.pone.0000140.

424   Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines.

425   Science **328**:1164-1168.

426   Clements, G. R., C. J. A. Bradshaw, B. W. Brook, and W. F. Laurance. 2011. The

427   SAFE index: using a threshold population target to measure relative species threat

428   Frontiers in Ecology and Environment **9**:521-525.

429   Clements, C. F., N. Worsfold, P. Warren, B. Collen, T. Blackburn, N. Clark, and O.

430   L. Petchey. 2013. Experimentally testing an extinction estimator: Solow's Optimal

431   Linear Estimation model. Journal of Animal Ecology **82**:345-354.

432   Collar, N. J. 1998. Extinction by assumption; or, the Romeo Error on Cebu. Oryx

433   **32**:239-244.

434   Collen, B., J. Loh, S. Whitmee, L. McRae, R. Amin, and J. E. M. Baillie. 2009.

435   Monitoring change in vertebrate abundance: the Living Planet Index.

436   Conservation Biology **23**:317-327.

437   Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with

438   variability in patch size and position. Theoretical Population Biology **48**: 333-360.

439   Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and

440   extinction parameters for endangered species. Ecological Monographs **61**:115-

441   143.

442   Di Fonzo, M., B. Collen, and G. M. Mace. 2013. A new method for identifying rapid

443   decline dynamics in wild vertebrate populations. Ecology and Evolution **3**:2378-

444   2391.

445   Di Stefano, J., M. A. McCarthy, A., York, T.J. Duff, J. Slingo, and F. Christie. 2013.

446   Defining vegetation age class distributions for multispecies conservation in fire-

447   prone landscapes. Biological Conservation **166**:111-117.

448   Gaston, K. J., and T. M. Blackburn. 2003. Macroecology and conservation biology.

449   Pages 345-367 in T.M. Blackburn, and K. J. Gaston, editors. Macroecology:

450   concepts and consequences. Blackwell Science, Oxford.

451   Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982.

452   Quasiextinction probabilities as a measure of impact on population growth. Risk

453   Analysis **2**:171-181.

454   Gregory R.D., and A. van Strien. 2010. Wild bird indicators: using composite

455   population trends of birds as measures of environmental health. Ornithological

456   Science **9**:3-22.

457   Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented

458   landscape. Nature **404**: 755-758.

459   IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species

460   Survival Commission, Gland, Switzerland and Cambridge, UK,

461   Jones, J. P. G., et al. 2011. The why, what, and how of global biodiversity indicators

462   beyond the 2010 target. Conservation Biology **25**:450-457.

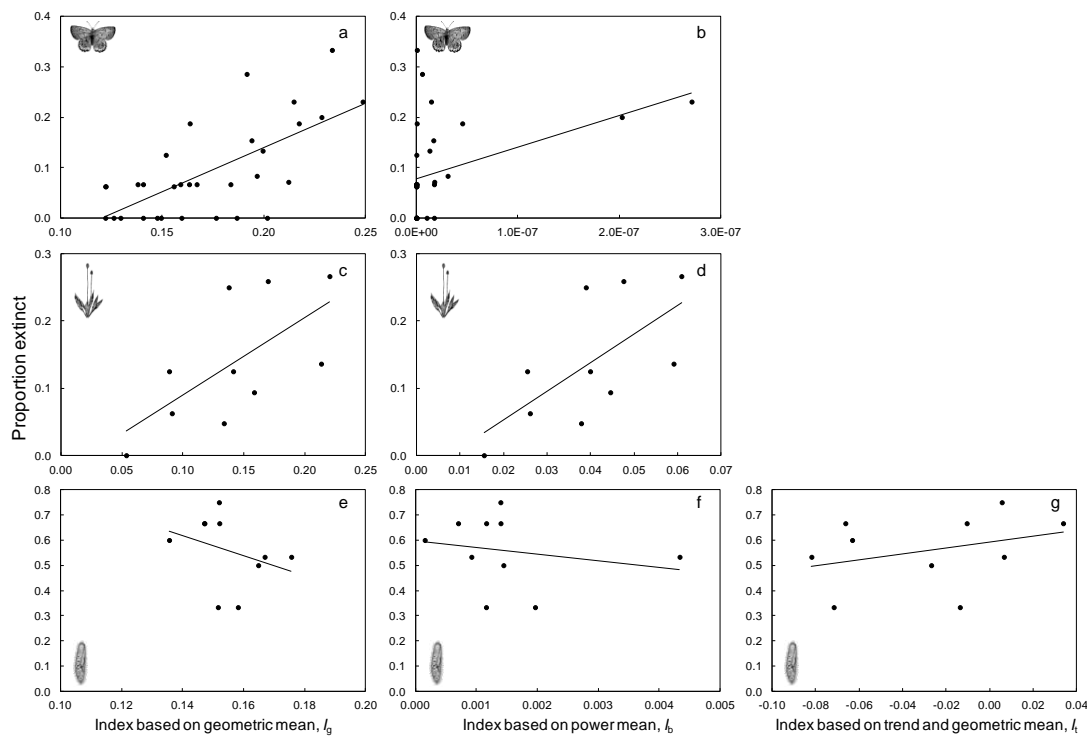463   Jost, L. 2006. Entropy and diversity. Oikos **113**:363-375.

464   Keith, D. A., and M. A. Burgman. 2004. The Lazarus effect: can the dynamics of

465   extinct species lists tell us anything about the status of biodiversity? Biological

466   Conservation **117**:41-48.

467   Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. Local species immigration,

468   extinction, and turnover of butterflies in relation to habitat area and habitat

469   isolation. Oecologia **137**:591-602.

470   Lande, R. 1993. Risks of population extinction from demographic and environmental

471   stochasticity and random catastrophes. American Naturalist **142**:911-927.

472   Loh, J., R. E. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos, and J. Randers.

473   2005. The Living Planet Index: using species population time series to track

474   trends in biodiversity. Philosophical Transactions of the Royal Society B-

475   Biological Sciences **360**:289-295.

476   Magurran, A. E. 2004. Measuring biological diversity. Oxford, Blackwell Science.

477   McCarthy, M. A., and C. Thompson. 2001. Expected minimum population size as a

478   measure of threat. Animal Conservation **4**:351-355.

479   McCarthy, M.A., G. E. Garrard, A. L. Moore, K. M. Parris, T. J. Regan, and G. E.

480   Ryan. 2011. The SAFE index should not be used for prioritization. Frontiers in

481   Ecology and the Environment **9**:486-487.

482   Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial

483   ecology. Ecology **83**:1131-1145.

484   Rout, T. M., D. Heinze, and M. A. McCarthy. 2010. Optimal allocation of

485   conservation resources to species that may be extinct. Conservation Biology

486   **24**:1111-1118.

487   Secretariat of the Convention on Biological Diversity. 2010. Global Biodiversity

488   Outlook 3. Secretariat of the Convention on Biological Diversity, Montreal,

489   Canada.

490   Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd edition. Freeman, New York.

491   Sutton, F. M., and J. W. Morgan. 2009. Functional traits and prior abundance explain

492   native plant extirpation in a fragmented woodland landscape. Journal of Ecology

493   **97**:718-727.

494   van Strien, A. J., L. Soldaat, and R. D. Gregory. 2012. Desirable mathematical

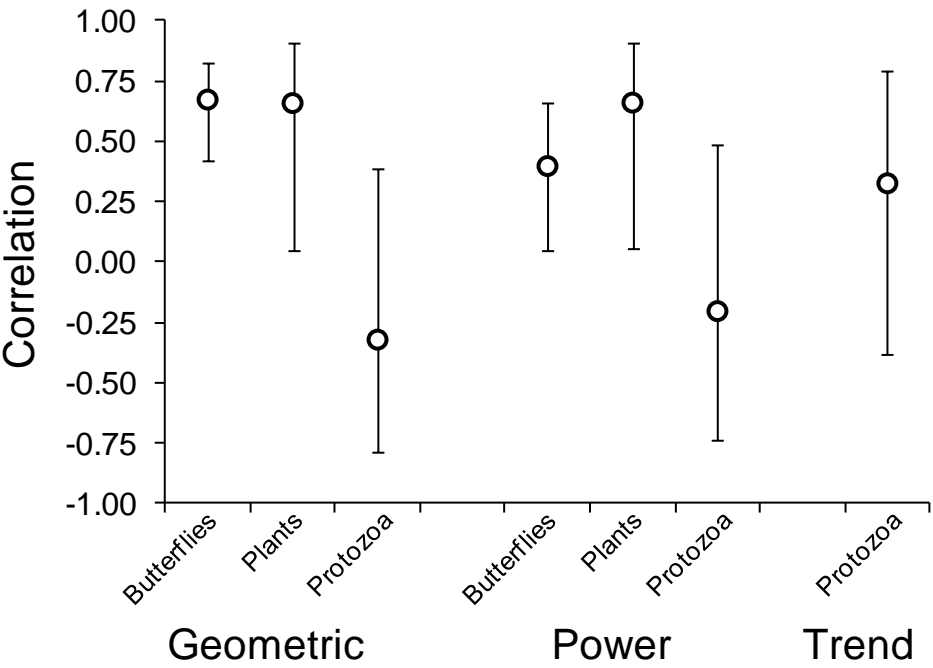495   properties of indicators for biodiversity change. Ecological Indicators **14**:202-208.

496

497   Figure 1. Relationship between the three different indices (I_g, I_b, I_t) and the proportion

498   of species going locally extinct for the three case studies: (a-b) for Lepidopetera; (c-d)

499   for woodland plants; and (e-g) for protozoan communities. Each point represents a

500   patch for the field studies (Lepidopetera and woodland plants) or the average of each

501   type of community for the protozoan. The lines are linear regressions. Correlation

502   coefficients with 95% confidence intervals are given in Fig. 2.

503   Figure. 2. Observed correlation between the three indices (I_g based on the geometric

504   mean; I_b based on the power mean; and I_t based on the geometric mean and trend) and

505   the proportion of species going extinct from a community. Results are shown for each

506   of the three different datasets (butterflies, plants, protozoa). The circles are the

507   observed correlation coefficients and the bars are 95% confidence intervals.

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509   Figure 3. Proportional changes in the probability of extinction from levels in 1970

510   based on changes in the Living Planet Index for birds (Baille et al. 2010) assuming

511   values for the geometric mean abundance in 1970 of 10,000, 100,000 or 1,000,000
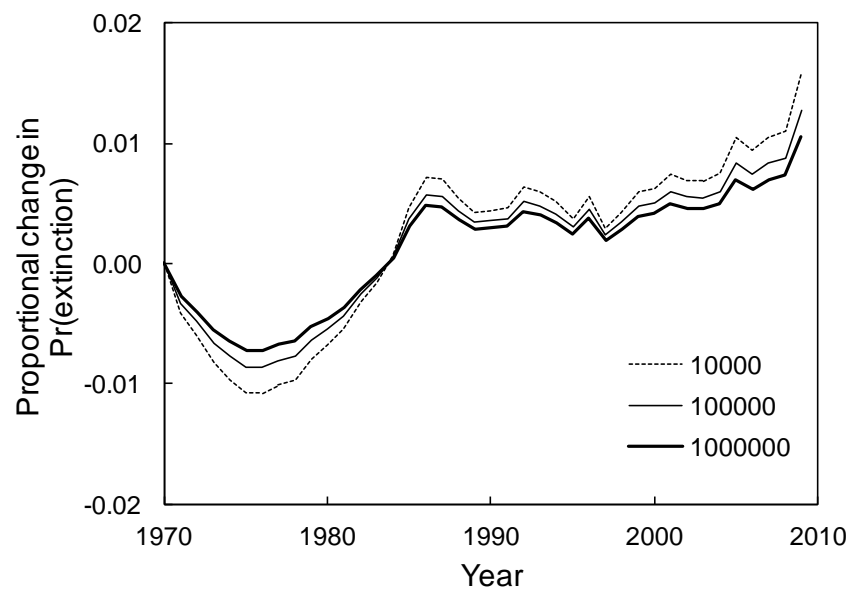
512   individuals.

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